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Response of Mountain Beaver (*Aplodontia rufa*) to Conspecifics in Their Burrow System

Abstract

The role of chemical communication in the social behavior of most burrowing rodents is largely unkown. We constructed artificial burrow systems to study interactions between mountain beavers (*Aplodontia rufa*). Though beavers exhibited scent marking behaviors, the marks did not prevent intruders from entering and exploring burrow systems. Encounters were agonistic and resident animals aggressively evicted intruders. We speculate that scent marking enhances the territorial confidence of the established mountain beaver.

Introduction

Mountain beavers (*Aplodontia rufa*) are generally regarded as a primitive fossorial rodent. Endemic to the Pacific Northwest, its range is associated with high rainfall and edaphic conditions that promote succulent vegetation and humid burrows (Voth 1968). The limits to their geographic distribution, however, are probably dictated by thermal requirements and adequate soil drainage, rather than forage availability (Beier 1989).

Burrow systems of mountain beaver have multiple openings and chambers and occur at any depth from beneath forest debris to 2 m below the surface (Feldhamer and Rochelle 1982). Chambers are used for nesting, food caches and fecal/refuse deposits (Voth 1968). Nest and feeding chambers form a hub from which burrows and other chambers radiate (Martin 1971). Nest chambers (50-60 cm diameter and 30-40 cm high) are packed with vegetation in which the animal constructs a small centrally located nest (Martin 1971). Food caches are stored in nearby chambers of similar or smaller size. Fecal/refuse chambers are generally located within a few meters (1-3) of the nest (Voth 1968). These vary in size and construction from blind tunnels to chambers larger than the nest chamber.

Mountain beavers travel through interconnecting burrows to forage (Martin 1971). Forays outside their burrow system are primarily nocturnal and generally within the proximity of a burrow entrance (Ingles 1959). Clipped plants are dragged or carried back to the burrow (Voth 1968).

Home ranges of mountain beavers often overlap and animals frequently share interconnecting runways (Martin 1971, Lovejoy and Black 1979). Nest and associated burrows, however, are the domain of an individual animal. Established animals rarely travel beyond their home ranges which vary in size from 0.03-0.2 ha. Dispersing subadults, however, may travel extensively, moving aboveground as well as through existing burrows (Martin 1971). Adult males may also extend their movements during the breeding season.

The role of chemical communication in the social behavior of mountain beavers is mostly unknown (Brown 1985). The only reported incidence of scent marking is of a captive male that marked a territory with urine (Wandeler and Pilleri 1965). The use of scent marks, however, would not be surprising. Although solitary, mountain beavers often live close to conspecifics (Lovejoy and Black 1979, Neal and Borrecco 1981). Territorial marking for defensive purposes might be expected because established nest sites appear to be a valuable resource to mountain beavers. Nests are rarely vacated voluntarily (Martin 1971), and nests which

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do become available are quickly occupied by other mountain beavers (Campbell *et al.* 1988).

We report the responses of resident mountain beaver to conspecific intruders encountered in an artificial burrow system. To our knowledge, this is the first description of encounters between these animals in a naturalistic setting.

Materials and Methods

Subjects

Mountain beavers were live trapped in the Capitol State Forest, Grays Harbor County, approximately 30 km from Olympia, Washington during July and August, 1991. After a minimum of 2 weeks habituation to captivity, animals that weighed >800 g when captured were air-shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. On arrival at Monell, all mountain beavers were given 14 days to adjust and establish a nest. Animals were individually caged (92 x 62 x 50 cm) under a changing light:dark cycle that reflected the natural day:night cycle of Olympia, Washington. Animals not involved in trials were maintained in these cages. Individual cages also consisted of an outside detachable bucket (30 cm dia. x 27 cm), used by mountain beavers as a nest. Access to this bucket was through a PVC pipe (15 cm dia. x 15 cm), which could be blocked by a sliding panel to lock animals in their nest. Aspen shavings (#1019; Buckshire Feeds, LTD, Lansdale, PA) spread on the cage floor were carried into the bucket by the resident mountain beaver for nesting material. Mountain beavers had free access to water and a 70:30 mixture of omnivore pellets and guinea pig food (RP 5635 Purina - Mozuri Zoo Feed "A" Omnivore and RP 5025 Purina–Guinea Pig Checkers, respectively; Buckshire Feeds LTD, Lansdale, PA). Slices of apple were also given to the animals 2 or 3 times a week.

Artificial Burrow System

Two burrow systems (Figure 1a) were constructed to monitor mountain beaver activity. Each system consisted of an open cage (204 x 92 x 64 cm) with an assortment of tunnels and chambers below (Figure 1b). Burrows were constructed of clear PVC pipe (15 cm dia.) and chambers consisted of polyethylene buckets (30 cm dia. x 27 or 35 cm) with plexiglass windows in the lids. Free access to food and water was provided in the open cage and aspen shavings covered the cage floor.

Mountain beavers to be introduced to the artificial burrow system were first secured in the detachable nest bucket attached to their individual cage. This nest bucket was then attached to the artificial burrow system (B-4; Figure 1b). Thus, each introduced mountain beaver had the option to retreat to its own established nest.

Procedure

Interactions between mountain beavers were observed in the morning at the beginning of the light period. Trials were concluded when animals returned to their respective nests and failed to emerge again for 15 min. Encounters were always between animals unfamiliar with each other. An intruder was never reintroduced to a system if it had previously encountered the resident animal.

A female mountain beaver was initially placed in each burrow system and allowed 48 hours to explore and establish a territory. Over the next 30 days, female (5) and male (13) mountain beavers were introduced into these occupied systems. Only one intruder was allowed to invade at a time and a minimum of 24 hours elapsed between encounters. After these initial tests the resident females were replaced with males. These males were allowed 48 hours to establish themselves and then we observed their response to an invading naive female. The original female occupant of each system was then reintroduced (72 hours after being replaced with a male). Initial encounters with the current male occupants were observed and then for 60 days we monitored animal and nest locations. This 60 day period overlapped the normal breeding season for mountain beaver. Finally, male occupants of each burrow system were removed and the females were observed for another 90 days.

Results and Discussion

When introduced to an unoccupied system, mountain beavers invariably vacated their attached nests and established residency in an artificial system. Subsequent animals readily accepted the nest and fecal chambers established by the original occupants. Though animals explored and exploited vacated systems, introduced mountain beavers never replaced a resident animal.

Mountain beaver responses to invading conspecifics in their burrow systems were always agonistic. Except for one male's intermittent acceptance

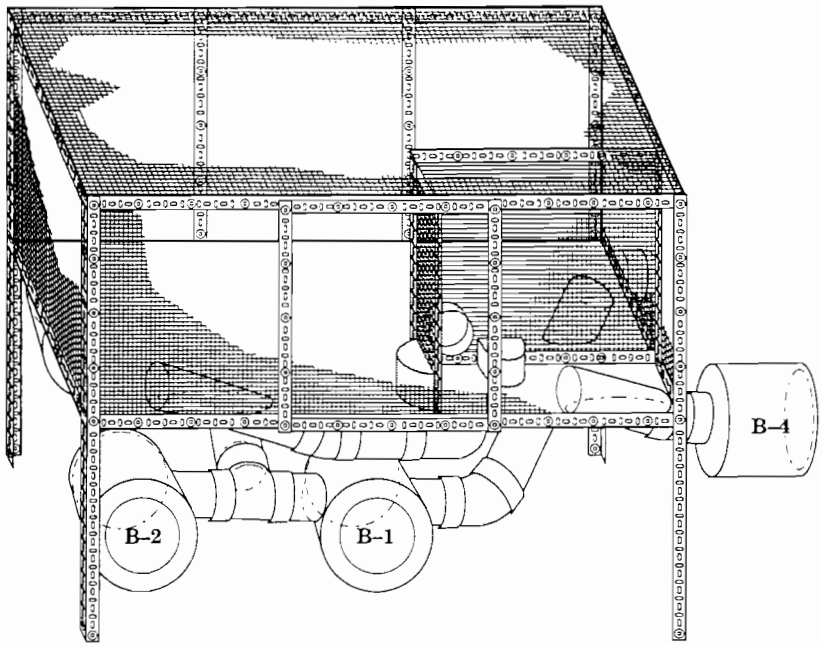

Figure 1a

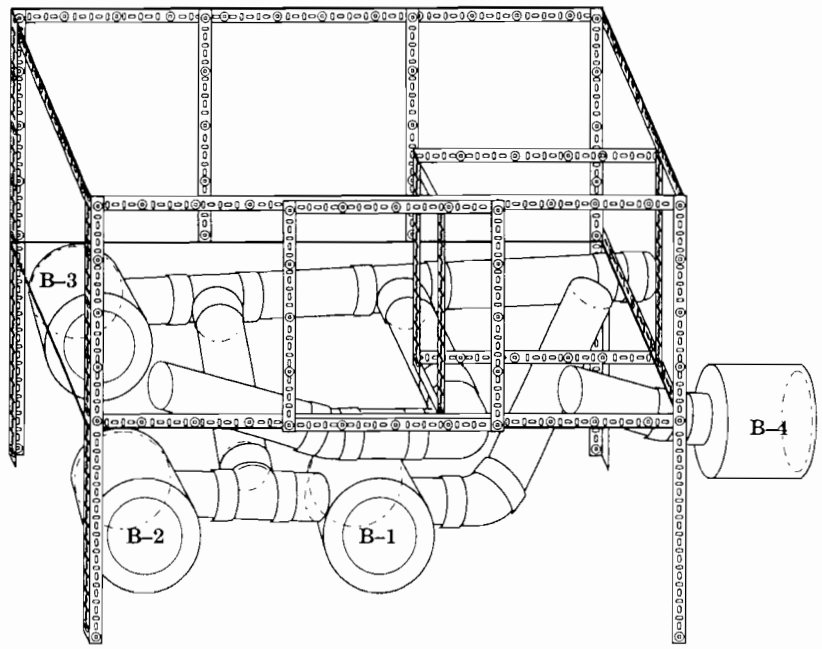

Figure 1b

Figure 1. Artificial burrow system constructed to resemble the solitary chambers and associated burrows of a mountain beaver. Systems consisted of an open cage (Figure 1a) and an assortment of tunnels and chambers below (Figure 1b).

of a female over a 3 day period during the breeding season, intruders were aggressively evicted by the resident animal. These observations are consisted with studies of mountain beaver under natural conditions which report nest sites to be occupied by a single animal (Martin 1971, Lovejoy and Black 1979). Aggressive behavior, however, appeared to be limited to the burrow system. Our artificial systems were small relative to a mountain beaver's home range; therefore, it was not possible to determine the response of mountain beavers to conspecifics in burrows outside the immediate vicinity of nests. However, mountain beavers that met outside the system ignored one another and resident animals never attempted to protect the food or water source on the surface. Mountain beavers introduced simultaneously in exclosures (1 ha) are not agonistic towards each other and initially may even share a nest (unpubl. data). Wild mountain beavers often travel the same

interconnecting runway system (Martin 1971, Lovejoy and Black 1979). The nature of encounters among animals along these runways is unknown.

Mountain beavers appeared to mark burrows outside their nest with odors, a behavior that might be expected from solitary animals that live in close proximity to conspecifics. Additionally, territorial marking in mammals is almost universally linked to agonistic behavior (Gosling 1990).

Rodents use urine, feces, specialized scent glands and vaginal secretion for chemical communication (Brown 1985). Mountain beaver may mark territories with secretions from sebaceous glands. Sebaceous gland secretions collect in hair follicles of the oral angle and lips (Quay 1965). Mountain beavers alternated between grooming and rubbing against chamber entrances and burrows, and while grooming they frequently put their feet to their mouths. Subsequently, marked areas were repeatedly sniffed by both the intruder and established animal. Several sciurid species (e.g. *Spermophilus* spp., *Tamias* spp.) use oral secretions from sebaceous glands for scent marking (Quay 1965).

Mountain beavers also produce a white secretion from the harderian and lacrimal glands near their eyes during some stressful situations (Hackman *et al.* 1990). In our study, white eye secretion was observed only on intruders when nose to nose with the resident animal. Animals that exhibited the secretion appeared frozen in place. This secretion may induce a tonic immobility, an adaptive defence reaction to attack (Hackman *et al.* 1990). Tonic immobility eliminates the movement stimuli that elicits an attack (Thompson *et al.* 1981), yet allows the animal to monitor its environment (Ewell *et al.* 1981). The secretion may also serve a semiochemical function. Secretion on the vibrissae may passively impart information about burrow usage (Hackman *et al.* 1990). Perhaps a submissive cue is passed to the aggressor.

Though mountain beaver marked burrows with scents these marks were not sufficient to prevent invasion by conspecifics. Intruders repeatedly explored occupied systems, rapidly exploiting any opportunity to establish themselves. Further, invaders left established nests of their own to occupy a nest recently abandoned by another animal. This continuous explorative and exploitive behavior may be reflective of similar behavior practiced by wild animals. An established female is reported to have traveled over 80 m to occupy the nest of a deceased male (Martin 1971). Additionally, extensive areas (40 ha) in which all mountain beaver have been removed are quickly invaded by other mountain beaver unless vacated nests are destroyed (Campbell *et al.* 1988).

Scent marking may serve to enhance the territorial confidence of mountain beaver. Established animals invariably retained possession of the burrow system and familiarity does not fully explain this dominance. Males ejected females after living in a burrow system for only 72 hours. Even though the ejected females had occupied the same system for 30 days and only 72 hours earlier had successfully evicted the current male. Established and intruding animals stopped to investigate marked areas. Recognition of odors may have enhanced the confidence of the established animal while weakening that of the intruder. Territorial confidence of European wild rabbits (*Oryctolagus cuniculus*) increases in the presence of odors from their scent glands (Mykytowycz *et al.* 1976). Presence of a rabbit's odor on otherwise neutral ground during encounters between rabbits generally dictates the dominant animal. Chin secretions are the most effective odor to stimulate confidence.

These observations provide some insight into the intra-specific encounters of mountain beavers in a naturalistic setting. Resident mountain beavers exhibited scent marking behaviors, however, these marks did not prevent intruders from entering and exploring a burrow system. Rather a vacated nest was quickly accepted by an intruding mountain beaver as its own. Occupied systems, however, were protected by the resident animals and encounters close to their nest were agonistic and the intruder aggressively evicted.

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